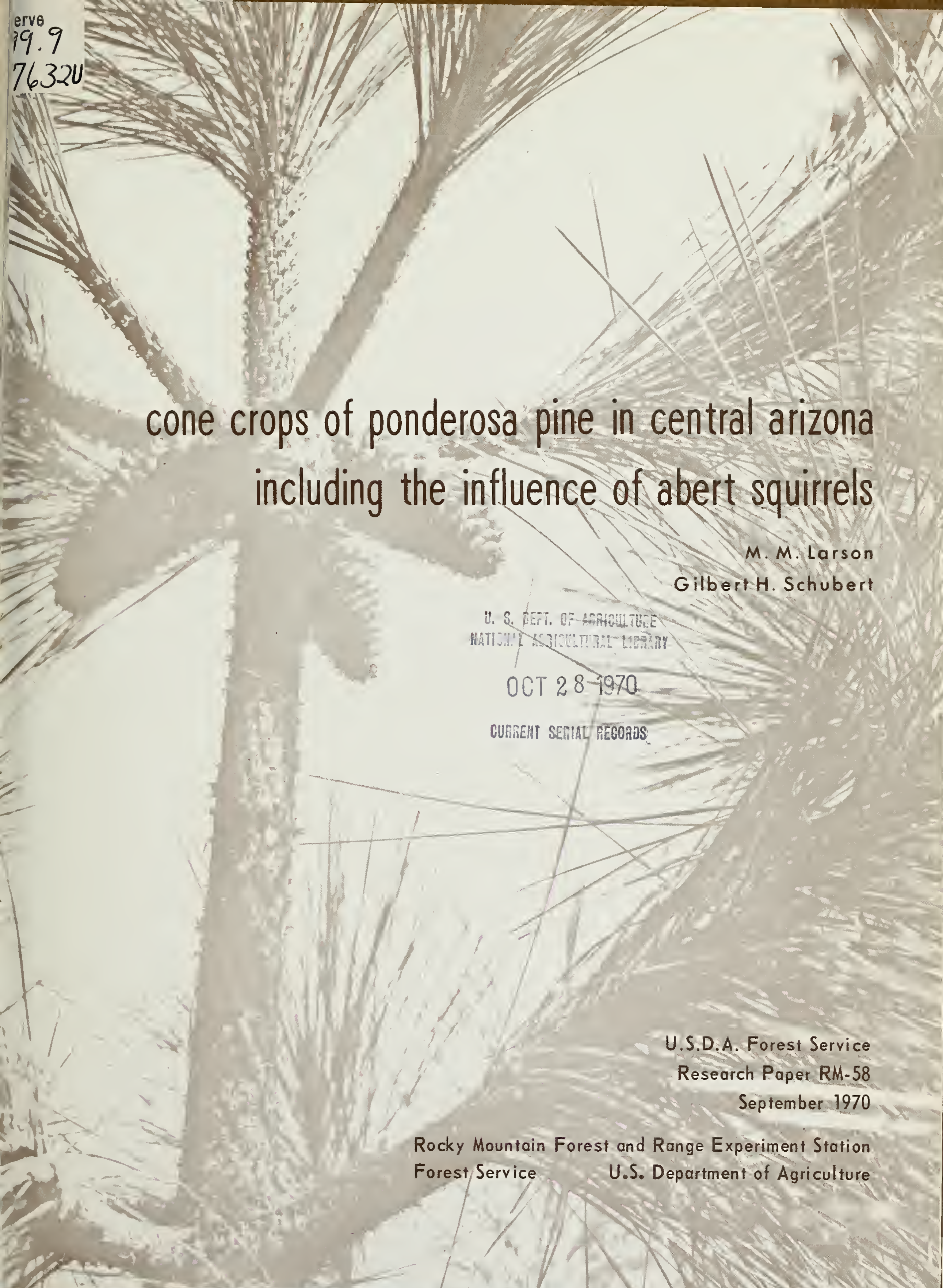

cone crops of ponderosa pine in central arizona including the influence of abert squirrels

M. M. Larson
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ABSTRACT

Large, vigorous, isolated ponderosa pines were the best cone producers in terms of seed quantity, quality, and frequency of bearing in the Southwest. Large cone crops occurred in 3 years out of 10. Trees 28 to 40 inches in diameter averaged 218 to 446 cones each per year. In contrast, trees 12 to 20 inches in diameter averaged less than 22 cones. The largest crop produced was 7,521 cones per acre in 1960, when 59 percent of the trees bore more than 100 cones each. Abert squirrels reduced the 10-year cone production by one-fifth. Conelet-bearing twigs clipped by squirrels provide a basis for predicting cone crop size.
Key words: *Pinus ponderosa*, conelets, cones, Abert squirrel

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Cone Crops of Ponderosa Pine in Central Arizona, Including the Influence of Abert Squirrels

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Cone Crops of Ponderosa Pine in Central Arizona, Including the Influence of Abert Squirrels

M. M. Larson and Gilbert H. Schubert

Introduction

Large quantities of seed are needed to maintain or increase productivity on about 7.5 million acres of commercial ponderosa pine (Pinus ponderosa Laws.) timberland in Arizona and New Mexico. Although ponderosa pines produce enough seed, time intervals between good crops and large differences in cone production between individual trees determine the amount of seed produced in an area. Since natural regeneration is still relied on to restock large areas, seed supply is a matter of primary importance.

This Paper reports on a 10-year investigation of the cone crops of ponderosa pine, and the influence of Abert squirrels (Sciurus aberti aberti Woodhouse) on these crops. In the study on the Fort Valley Experimental Forest, we determined the types of trees bearing cones, size and frequency of cone crops, seed dissemination, and the detrimental influence of the seed-eating and twig-clipping activities of the Abert squirrel. We also found that the abundance of conelets [2] on clipped twigs indicates the size of the ensuing seed crop.

[2] *In this paper the term "conelet" refers to ovulate strobili from the time of their appearance in late spring until their fertilization the following spring. After fertilization, the term "cone" is used. Clipped twigs may have both 1-year-old conelets and new flower buds. Only the 1-year-old conelets were counted, since new flower buds could not be distinguished at this stage from vegetative buds.*

Detailed descriptions of flowering and cone development of ponderosa pine have been reported by Roeser (1941) and Gifford and Mirov (1960). Long-term studies of cone production were reported for ponderosa pine in California (Fowells and Schubert 1956), in Montana (Boe 1954), and in Washington (Daubenmire 1960). In the Southwest, Pearson (1912, 1923, 1950) identified the types of trees that bear good cone crops, and indicated the kind and number of trees needed to provide an adequate seed supply for regeneration.

Adequate stands of natural regeneration are infrequent; seed supply may be a limiting factor at times, but our knowledge is inadequate. Abert squirrels are known to destroy large numbers of cones (Keith 1965), but a long-term quantitative evaluation of damage has never been made. This study revealed that squirrel impact can indeed be substantial, even in periods of low populations.

Conduct of the Study

Experimental Area

The study was conducted on a 10-acre plot in the G. A. Pearson Natural Area near Flagstaff. The virgin stand contained 253 trees over 12.0 inches in diameter breast high (d.b.h.). The trees averaged 22.7 inches d.b.h. and were mature and overmature (fig. 1). Twelve trees that died during the study were excluded from the analysis.

Figure 1.--Ponderosa pines in the G. A. Pearson Natural Area of the Fort Valley Experimental Forest.

There were very few trees 8 to 12 inches d.b.h. Dense patches of saplings and small poles of 1919 origin occupied most of the ground space not covered by crowns of the larger trees.

The site index is about 85 feet at base age of 100 years. The plot is nearly level, with a slight south-facing aspect. The silty clay loam soil was derived from basalt and is nearly neutral in pH. Precipitation averages about 23 inches annually. The wettest months are July and August. The temperature ranges from a mean maximum of 88.2° F. in July to a mean minimum of -11.2° F. in January. The hottest and coldest temperatures were 96° F. and -37° F.

Tree Classifications

All trees were classified as to age-vigor (Thomson 1940), tree position, dominance, and squirrel damage (table 1). The diameter of each sample tree was measured in the fall of 1954 and in spring of 1965 for a 10-year growing period.

Cone Counts

Three classes of cones were collected and counted in each of the 10 crop years. The first class consisted of immature cones cut by squirrels beginning about mid-June and ending in late October (fig. 2). These collections and counts were made at about monthly intervals. Cones cut by squirrels were easily identified since the green cone scales were chewed off and the seeds eaten. No cones or seeds are stored by Abert squirrels.

The second class consisted of normal undamaged cones. These cones were collected and counted in the spring following seed fall. Since not all cones are released during the winter months, additional collections were made during the summer with a final collection prior to the drop of the next crop.

Table 1.--Tree classifications and descriptions of subclasses

Tree classifications	Description
Age-vigor[1]	
Age II	Young "blackjacks" of sawtimber size
Age III	"Intermediates" or young "yellow pines" (mature)
Age IV	Old "yellow pines" (overmature)
Vigor A	Full vigor, crown 55 to 70 percent of tree height
Vigor B	Good to fair vigor, crown 35 to 55 percent of tree height
Vigor C	Fair to poor vigor, crown 20 to 35 percent of tree height
Vigor D	Very poor vigor, crown less than 20 percent of tree height
Tree position	
Isolated	Trees isolated, free to grow on all sides
Open	Open grown trees but near a group of trees
Marginal (border)	Marginal trees growing on the edge of a group
Interior	Interior trees growing inside a group
Tree dominance	
Dominant	Trees with crowns extending above the general crown level
Codominant	Trees with crowns forming the general crown level
Intermediate	Trees shorter but crowns extend into the general crown level
Suppressed	Trees with crowns entirely below the general crown level
Squirrel damage	
None	No visible crown damage
Light	Some twig cutting apparent but crowns dense
Medium	Moderate twig cutting, noticeable crown thinning
Heavy	Crown very thin due to twig cutting

[1]Based on Keen's Tree Classification as modified for the Southwest by Thomson (1940). Age class I "young blackjacks" less than 12 inches diameter were not included in the study.

Figure 2.--Ponderosa pine cones with scales and seed removed by Abert squirrels. From left to right, cones were collected in 1956 on June 19, July 9, August 2, and October 23, respectively.

Most trees shed all except insect-infested cones within 1 year. Although four trees consistently retained a few cones for more than 1 year, they introduced an insignificant error into yearly totals.

The third class consisted of insect-infested cones. These cones were usually small, deformed, pitchy, and contained exit holes, principally of the ponderosa pine cone beetle (Conopthorus scopulorum Hopk.). These insect-damaged cones often persisted on the tree for more than 1 year, so the cone year could not be determined precisely.

All three classes of cones were credited to the tree from which they appeared to have fallen. Crown shape, tree lean, and prevailing wind direction were all considered in assigning cones to their probable source tree. This tree assignment was also facilitated by the cone crop rating of heavy, medium, light, or none given each tree prior to cone release.

Twig Counts

Twigs (branch tips) clipped by Abert squirrels were counted in May or early June of each year (figs. 3, 4). These clipped twigs bore distinctive tooth marks on the cut end, which made them easy to distinguish from the few wind-broken twigs found in the area. Because twigs fell directly beneath the parent tree, they were easy to credit properly. Very few twigs were clipped by the squirrels from late May to early December.

Figure 3.--A ponderosa pine twig (lateral shoot or branch tip) with a conelet (unfertilized female strobilus), and a peeled branch section. Abert squirrels first cut off the twig from the branch section, then eat the tender inner bark.

Figure 4.--Crown of a ponderosa pine tree, 16 inches d.b.h., heavily damaged by Abert squirrels. This tree was severely clipped every year during the 10-year study.

Prediction of Cone Crops

Each twig clipped by squirrels was examined and the number of 1-year-old conelets recorded (fig. 3). These conelets would have matured by October. It was assumed that Abert squirrels clip twigs without regard to the presence of conelets, and that similar crown areas were attacked each year. Most twigs appeared to be cut from the upper part of the crowns. The ratio of conelet-bearing to total clipped twigs was then related to the number of cones produced that fall.

Seed Counts

Fifty seed traps, each 3.3 feet square (1/4 milacre), were randomly located on the plot in 1956 (fig. 5). Seeds caught in the traps were counted each of the 10 years. Seed quality was determined in some years by floating off the hollow seeds in acetone. Germination tests were made on three crops. The time of seed fall was determined for the 1965 crop by counting the trapped seed frequently after the cones started to open.

Results and Discussion

Types of Trees Bearing Cones

The largest trees produced the most cones. Trees 36 to 40 inches d.b.h. averaged 446 cones per tree per crop, compared to six cones produced by trees 12 to 16 inches d.b.h. (table 2). Tree diameter accounted for about 94 percent of the variation in cone production (average annual cone production per tree = -299.82 + 18.19 d.b.h.). Trees under 24 inches d.b.h. at Fort Valley averaged less than 100 cones per crop, which was similar to the results obtained for ponderosa pine in California (Fowells and Schubert 1956). However, trees 36 to 40 inches d.b.h. produced about twice as many cones as California trees in the same size class.

Largest cone crops occurred on trees that were free to grow on all sides (table 2). These trees, classified as "isolated," averaged 274 cones per crop compared to 42 for "interior" trees within a group. Pearson (1912, 1923) also noted the superior

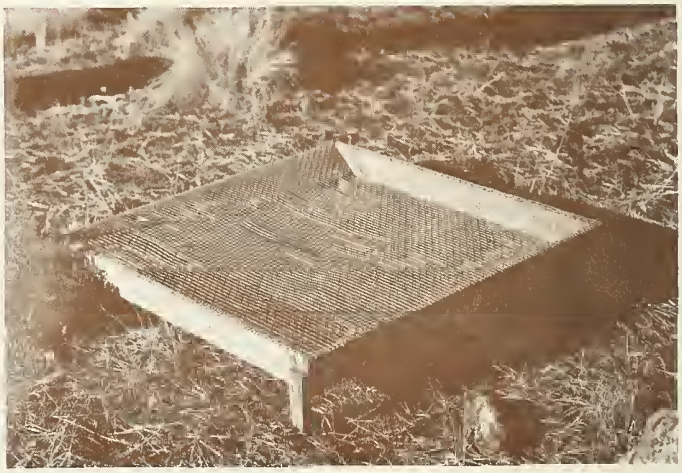

Figure 5.--A 1/4-milacre trap used to sample seed fall.

Table 2.--Distribution of trees and cone production by several classification criteria on the 10-acre Fort Valley Experimental Forest plot during the 10-year period, 1956-65

Classification	Trees	Total cones produced	Crops with per-tree average greater than: 5 cones	Crops with per-tree average greater than: 100 cones	Average annual cone production per tree
	- - - - - - - -	Number	- - - - - - - -		
DIAMETER (Inches)					
12-16	34	1,922	2.1	0.1	6
16-20	51	10,461	4.5	.6	21
20-24	55	41,238	7.7	2.1	75
24-28	62	86,485	8.7	3.6	139
28-32	26	56,791	9.3	4.4	218
32-36	11	33,704	9.7	5.7	306
36-40	2	8,929	10.0	6.5	446
AGE-VIGOR					
II D	13	1,915	2.4	.4	15
C	37	8,859	4.4	.7	24
B	34	13,149	5.0	1.1	39
A	5	2,363	6.2	1.4	47
III D	28	15,246	6.6	1.8	54
C	47	56,445	8.1	3.0	120
B	36	63,313	8.7	3.8	176
A	7	12,911	9.7	4.4	184
IV D	4	2,789	8.2	2.0	70
C	18	22,565	8.1	3.2	125
B	10	31,011	9.8	5.6	310
A	2	8,964	10.0	6.5	448
STAND DENSITY					
Interior	50	21,059	5.5	1.2	42
Marginal	135	121,885	6.8	2.2	90
Open	49	77,395	7.9	3.5	158
Isolated	7	19,191	8.3	5.0	274
SQUIRREL DAMAGE					
Heavy	25	13,470	--	--	54
Medium	48	47,632	--	--	99
Light	156	158,692	--	--	102
None	12	19,736	--	--	164
TREE DOMINANCE					
Suppressed	30	3,061	3.4	1.7	10
Intermediate	53	22,546	5.3	1.2	43
Codominant	67	58,932	7.3	2.4	88
Dominant	91	154,991	8.4	3.8	170
Total or Average	241	239,530	--	--	99

Note: "--" indicates negligible.

cone productivity of isolated trees over those growing within a stand. Due to their greater numbers, "marginal" trees around the exterior of stands produced the greatest quantity of cones.

Dominant trees bore the most cones (table 2). They rate this distinction on both a stand and on individual-tree basis. Since the dominant trees were also largest in diameter, part of this extra

cone production must be related to their superior size. For example, when the effect of tree diameter was held constant in a least-squares analysis, the differences in cone production between dominance classes was less pronounced. In an even-aged stand, dominance may have a much greater independent effect than in an all-aged stand where shorter trees on the edge of a group often have large cone-bearing crowns.

Trees with the least amount of squirrel damage bore the most cones (table 2). Trees with undamaged crowns produced over three times as many cones per crop as trees with heavy crown damage. Nearly 65 percent of the trees had light squirrel damage, and they produced 66 percent of the 10-year total.

Cone production varied significantly among age-vigor classes (table 2, fig. 6). The largest crops per tree were borne by the oldest, most vigorous trees; thus the older "yellow pines" (age class IV) of good vigor were excellent producers. The poorest producers were age class II "blackjack" trees and

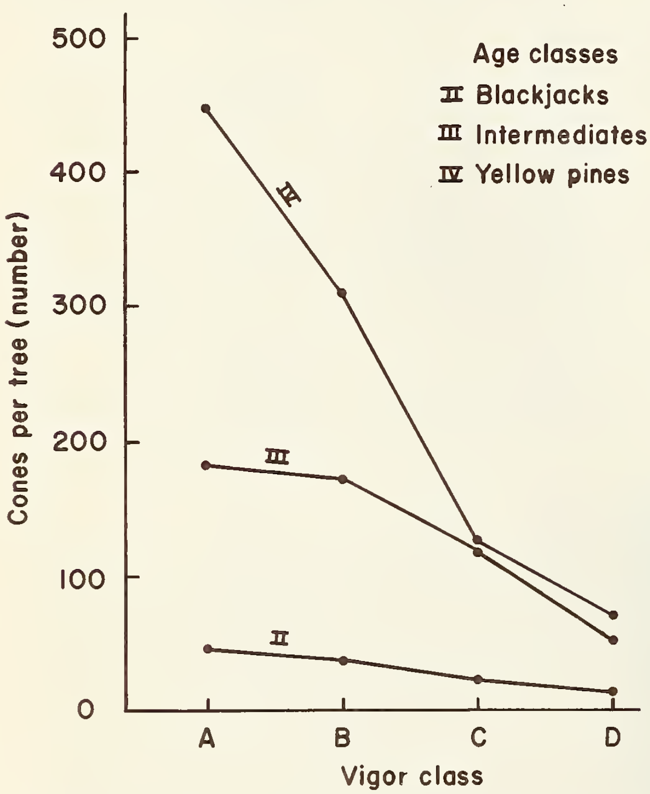

Figure 6.--Effect of vigor on average annual cone cone production per tree for trees in each age class.

trees of poor vigor. On a stand basis, trees classified IIIA and IIIB produced the most cones, partly due to their greater occurrence. Although ponderosa pines can produce cones at age 16 and continue to produce at age 350 (Curtis 1955), it is the large, mature trees that produce the heavy crops.

The record total 10-year production by an individual tree was 5,677 cones. This tree, 33.6 inches d.b.h. and age-vigor class IVB, also produced the most cones in a single year, 1,887 in 1960.

Size of Annual Cone Crops

The annual production of undamaged cones varied from 80 to 7,046 per acre (table 3). The greatest number of cones, a "bumper" crop, was produced in 1960. Based on an average of 37 good seeds per cone, this "bumper" crop was equivalent to 263,000 seeds per acre (about 22 pounds). Data are unavailable for a direct comparison with the 1918 seed crop, but based on Pearson's (1950) estimate of a seed to seedling ratio of 100:1, the 1918 crop may have been up to four times greater than the 1960 seed crop.

Cone crops in 1956 and 1965 were rated as large (table 3), but were about half the bumper crop in 1960. Cone crops were small in 5 of the 10 years.

Frequency of Good Cone Crops

Large ponderosa pine cone crops have been observed on the Coconino and Kaibab National Forests in 1913, 1918, 1927, 1936, 1942, 1945, 1954, 1956, 1960, and 1965. Therefore, during this 52-year period, large cone crops occurred at intervals of about 5 years.

Frequency of Cone Bearing by Individual Trees

During the 10-year period, nearly all trees produced at least one cone; only 6 percent of the trees produced fewer than 100 cones. On the other hand, 65 percent of the trees produced at least one crop that exceeded 100 cones, and 95 percent had at least one crop that exceeded five cones. Forty trees (16.6 percent) had five or more crops that exceeded 100 cones per tree, while seven trees produced eight such crops.

Table 3.--Annual ponderosa pine cone production per acre, number of trees bearing more than 5 and more than 100 cones, and number of cones destroyed by Abert squirrels on the 10-acre Fort Valley plot

Year	Total cones per acre	Cones destroyed by squirrels		Undamaged cones	Trees bearing more than:		Cone crop rating[1]
					5 cones	100 cones	
	Number	Number	Percent	Number	- - Percent - -		
1956	4,503	870	19.3	3,633	83	52	Large
1957	2,675	806	30.1	1,869	85	23	Medium
1958	741	194	27.5	547	67	5	Small
1959	316	236	74.7	80	36	2	Small
1960	7,521	475	6.3	7,046	90	59	Bumper
1961	936	3	.3	933	65	10	Small
1962	464	310	66.9	154	54	2	Small
1963	1,792	1,137	63.5	655	56	20	Small
1964	1,691	648	38.4	1,043	64	17	Medium
1965	3,730	403	10.8	3,327	78	48	Large
Average	2,437	508	20.9	1,927	68	24	

[1]Based on production of undamaged cones as follows: small, less than 1,000; medium, 1,000 to 3,000; large, 3,000 to 6,000; bumper, greater than 6,000.

The greatest number of trees bore cones during the 1960 bumper seed year. In that year, 90 percent of the trees bore at least five cones and 59 percent bore at least 100 cones (table 3).

Frequency of cone bearing was strongly correlated with tree diameter (table 2). The correlation coefficient of frequency to diameter was 0.94 for crops exceeding five cones per tree and 0.99 for those exceeding 100 cones. Individual trees over 28 inches in diameter averaged 9.7 crops over five cones and 5.5 crops over 100 cones during the 10-year period. In contrast, trees under 20 inches d.b.h. averaged only 3.3 crops over five cones and 0.4 crop over 100 cones.

Frequency of cone bearing also increased with increased growing space (table 2). Isolated trees had the greatest number of crops, while interior trees had the least.

Comparisons by dominance classes showed that dominant trees bore cones more frequently than other classes. Although a few intermediate and suppressed trees bore cone crops exceeding 100 cones per tree, the low frequency rate indicates that these trees are poor cone producers.

Cone crop frequency increased with age, but decreased with decreased tree vigor (table 2). In general, IVA trees produced a large crop most frequently and IID trees the least. Only IVA and IVB trees produced large crops over 50 percent of the time. None of the class II "blackjacks" contributed much to the three large cone crops during the 10-year period.

Cones Destroyed by Squirrels

The proportion of cones cut by Abert squirrels varied significantly during the period 1956-65 (table 3). The number of cones cut varied from 3 per acre in 1961 to 1,137 in 1963. The proportion of the cone crop cut by squirrels varied from 0.3 percent in 1961 to 74.7 percent in 1959.

The number of cones cut by squirrels was not closely related to the size of the total crop. The medium cone crop in 1963 was reduced to a small crop when squirrels cut over double their yearly average. In general, a higher proportion of the crop was cut during poor than during good seed years. Heavy losses of ponderosa pine cones to tree squirrels have been reported in Colorado (Roeser 1941), Idaho (Squillace 1953), and California (Fowells and Schubert 1956).

Abert squirrels reduced the total 10-year cone production at Fort Valley by 21 percent (table 3). In addition, many conelets and flower buds were destroyed when squirrels clipped twigs for food. Although the loss by twig clipping averaged only 22 conelets per acre, it raised the total destroyed by an extra 1 percent. Squillace (1953) reported

a 9 percent loss of conelets due to twig clipping by squirrels in Idaho.

Cone cutting by squirrels was strongly correlated (r = 0.980) with number of cones per tree. The largest trees produced and lost the most cones (fig. 7). Although small trees lost a higher proportion of their cones, the large trees, with more cones available, lost the most.

Cone cutting varied widely among trees. Some trees lost no cones while some lost 80 percent. The highest number cut from a single tree was 1,293 cones in 1964. Several trees lost over half of their total 10-year production to squirrels, while other trees produced several thousands of cones and lost less than 10 percent.

No reason was found for this preference of cones from one tree to another.[3] In this study, the portion of cones lost to squirrels was not affected by age-vigor, ground position, dominance, or squirrel damage to crowns. Tree nutrition may be a factor. Asher (1963) reported that squirrels preferred the cones of fertilized slash pine trees over those of unfertilized trees.

Cone cutting can be prevented by placing an 18-inch-wide metal band around the trunks of seed trees (Tackle 1957, Krugman and Echols 1963). The bands prevent the squirrels from climbing the trunks, but the tree crown must also be at least 7 feet from that of unbanded trees. Control of squirrel populations by hunting has been of limited success. Goshawks may be a predator of squirrels in some areas (Reynolds 1963).

[3] *Ralph A. Read found that jackrabbits seemed to prefer trees from certain seed sources in his provenance study. (Unpublished data on file at Rocky Mt. Forest and Range Exp. Sta., U. S. Forest Serv., Lincoln, Nebr.)*

Cones Infested by Insects

From 1958 through 1964, 3,404 cones were found to infested with insects. Insect-infested cones were not included in the yearly totals because they often persist for more than 1 year. They would have increased the total number of cones by

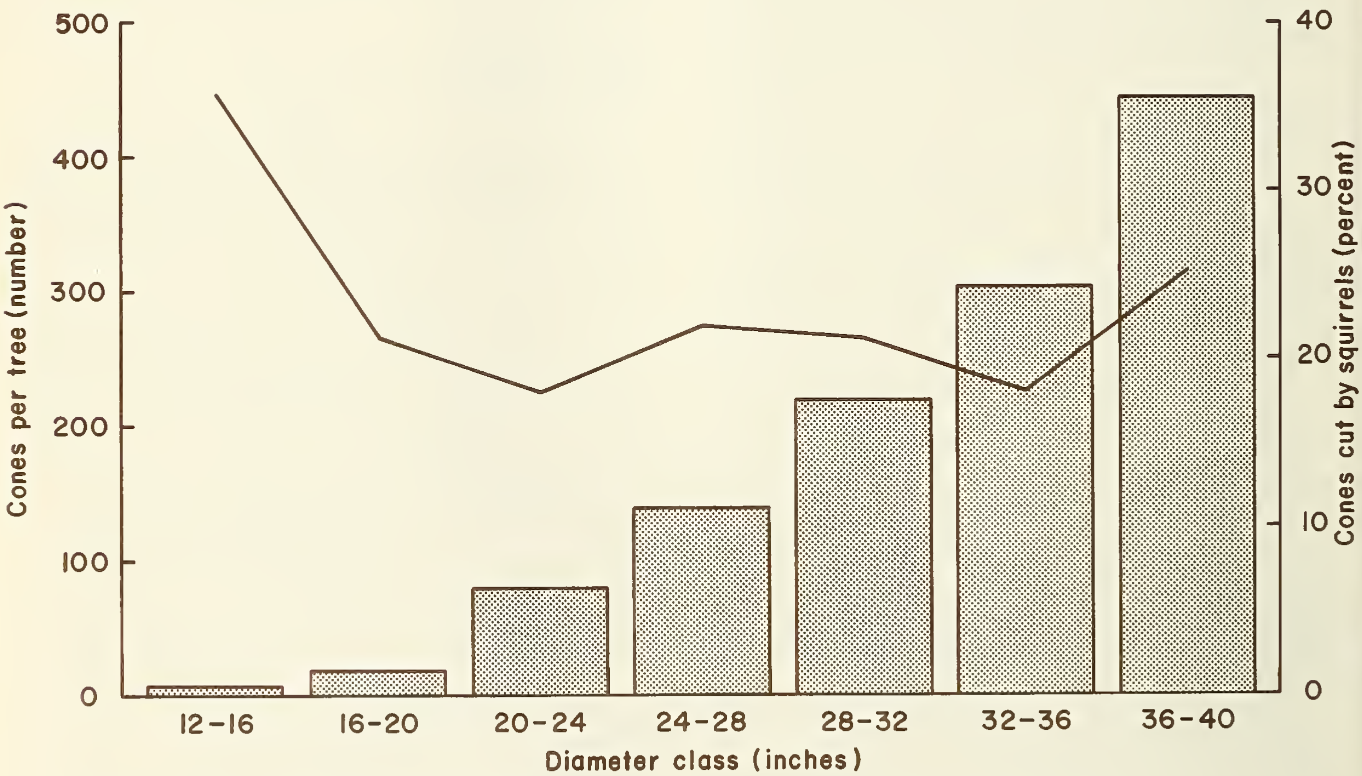

Figure 7.--Average yearly cone production per tree (bars) and the average percentage of cones cut by Abert squirrels (line) for trees in each diameter class.

Table 4.--Annual ponderosa pine seed production, estimated seed production, and twig cutting by Abert squirrels on the 10-acre Fort Valley plot

Year	Total seed in traps[1]	Filled seed[2]	Estimated total seed production per acre	Twigs cut by squirrels (per acre)			
				Total	With conelets		Conelets per twig
	Number	Percent	Number	Number	Number	Percent	Number
1956	1,331	--	106,480	286	31	10.7	1.6
1957	688	--	55,040	605	37	6.1	1.7
1958	16	--	1,280	595	5	.9	1.3
1959	13	--	1,040	357	2	.6	1.4
1960	3,292	81	263,360	231	23	10.0	1.7
1961	69	45	5,520	592	12	2.0	--
1962	37	22	2,960	140	3	2.2	1.7
1963	271	17	21,680	125	5	4.2	1.7
1964	185	10	14,800	154	10	6.2	1.7
1965	1,568	65	125,440	136	10	7.0	1.8
Average	747	40	59,760	322	13.8	5.0	1.6

[1]Fifty traps, each 3.2 x 3.2 feet or 1/4 milacre.
[2]Seeds placed in acetone and "sinkers" counted as filled.
Note: "--" indicates not measured.

2.5 percent, however. Fifteen of the 241 study trees accounted for 63 percent of the total infested cones. These "insect preferred" trees were characteristically dominant or open grown, and averaged 28 inches d.b.h., 5 inches larger than the average for the plot.

Larvae of the cone beetle (Conopthorus scopulorum Hopk.) were found in infested cones, but other cone insects may also have been present. Pearson (1950) reported that cone beetles are especially serious pests in the lower portions of the pine type, where they have completely destroyed cone crops. A method to control cone beetles on ponderosa pine has not been developed, but the systemic insecticide "bidrin" implanted in trunks gave good control of cone insects in slash pine (Merkel 1969).

Twig Cutting by Abert Squirrels

Squirrels clipped from 125 to 605 twigs per acre annually (table 4). It is not known how many twigs were available for clipping. Relatively few were clipped during the final 4 years of the study.

Trees with "heavy" crown damage in 1956 continued to be heavily clipped throughout the study. These trees lost an average of 33 twigs per year, compared to four twigs per year for trees with little to no crown damage. Twig clipping by squirrels was similar among trees with respect to tree position, dominance, diameter, and age-vigor class.

The most severe twig clipping sustained by an individual tree totaled 1,869 twigs for the 10-year period. This tree, 23.1 inches d.b.h. and of age-vigor class IIIC, lost 656 twigs in 1959, a record number during a single year. The squirrel population at Fort Valley was very high from 1940 to 1945 (Keith 1965), and Pearson (1950) observed that it was not unusual to find as many as 1,000 twigs under a single tree. Pearson (1950) also noted decreased diameter growth of individual trees severely damaged by squirrels. During the present study, one tree just outside the plot boundary died after repeated heavy twig clipping by squirrels.

Every tree in the study area was "tasted" by squirrels at least once during the 10-year period. Occasionally, individual trees suffered heavy twig clipping in 1 year, but then were virtually ignored in other years. Repeated clipping of the same tree year after year was the rule, however: one-third of the total twigs clipped during the study came from only 13 trees.

One might expect the number of twigs clipped each year would be related to the number of cut cones, and that these yearly cuttings of twigs and cones would indicate trends in the size of the squirrel population of the area. However, the number of clipped twigs (table 4) was not related to the number of cut cones (table 3) and neither of these

may accurately reflect the size of the current squirrel population. The twigs are clipped during the winter and spring, while the cones are cut during the summer and fall. Individual Abert squirrels range over about 18 acres during the summer but only 5 acres during the winter (Keith 1965). Thus, the squirrel population of the surrounding area would largely determine the degree of cone and twig clipping within the 10-acre study plot. A high winter mortality of a large squirrel population could result in many clipped twigs but few cut cones the following summer. Also, the area was open to squirrel hunting each fall.

The percentage of cut twigs with one or more conelets ranged from 0.6 to 10.7 percent (table 4). The number of conelets per conelet-bearing twig usually averaged 1.6 to 1.8.

Prediction of Size of Cone Crops

The percentage of twigs with conelets found each spring was related to the size of the cone crop that followed (fig. 8). When 7 percent or more of the twigs bore conelets, large cone crops followed, whereas a low percentage of conelet-bearing twigs always preceded small crops. The approximate number of cones per tree can be estimated from figure 8 by dividing the number of cones per acre (Y-axis) by the number of trees per acre bearing cones. In our study, an average of 25 trees per acre bore cones during the 10-year period.

In the construction of figure 8, the number of cones cut by squirrels was included in the total cones, since yearly depredations vary widely. When only the number of cones that survived to maturity

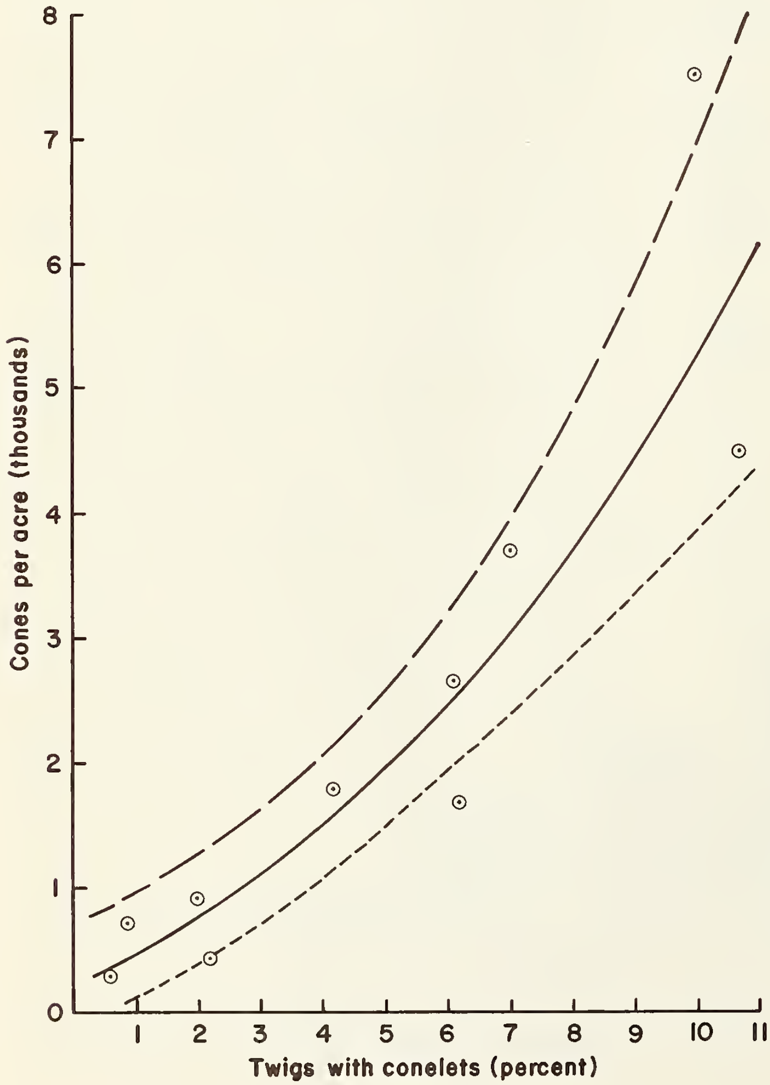

Figure 8.--Relationship between total cone production per acre and the percentage of twigs with conelets found during the spring preceding the maturation of cones. The calculated regression line is $Y = (16.41 + 5.64x)^2$, $F = 47.41^{**}$. Dashed lines indicate upper and lower 95 percent confidence limits.

were considered, the relationship with the yearly percentage of twigs with conelets was less close.

Prediction of seed crops by counting conelets (ovulate strobili) on selected branches or trees has been attempted with larch (Roe 1966), longleaf pine (Shoulders 1967), loblolly pine (Trousdell 1950), pinyon (Little 1939), Douglas-fir (Allen 1941, Roeser 1942), red pine (Lester 1967), and ponderosa pine (Roeser 1941, Maguire 1956). Results ranged from very good to poor. In general, crop failures and light crops were predicted with considerable success, but predicted heavy crops often failed because the conelets died before they matured.

Mortality of conelets is greatest during the first growing season after emergence; losses average 64 percent in ponderosa pine (Roeser 1941), 60 percent in red pine (Lester 1967), and 87 percent during one season in slash pine (Merkel 1961). Unfavorable weather and insects were the major causes of conelet mortality. It appears that large crops can be accurately predicted only when conelets are counted after the first growing season (as in this study) and when cone cutting by squirrels is low.

Some investigators have predicted cone crops on the basis of temperature. For example, Maguire (1956) found that above-average temperatures in April and May stimulated flowering the following spring, and Daubenmire (1960) also reported that above-average temperature during the summer that flower initials are formed improved cone production 2 years later. No attempt was made in our study to relate weather data with cone production.

Correlations

The 10-year cone production of individual trees was significantly correlated with the percentage of twigs with conelets ($r = 0.429^{**}$), although the r^2 is only 18 percent. The following measurements were not significantly correlated at the 5 percent level: total cones vs total twigs; total twigs vs percent twigs with conelets; total twigs vs percentage of cones cut by squirrels; percent twigs with conelets vs percentage of cones cut by squirrels; and total cones vs percentage of cones cut by squirrels.

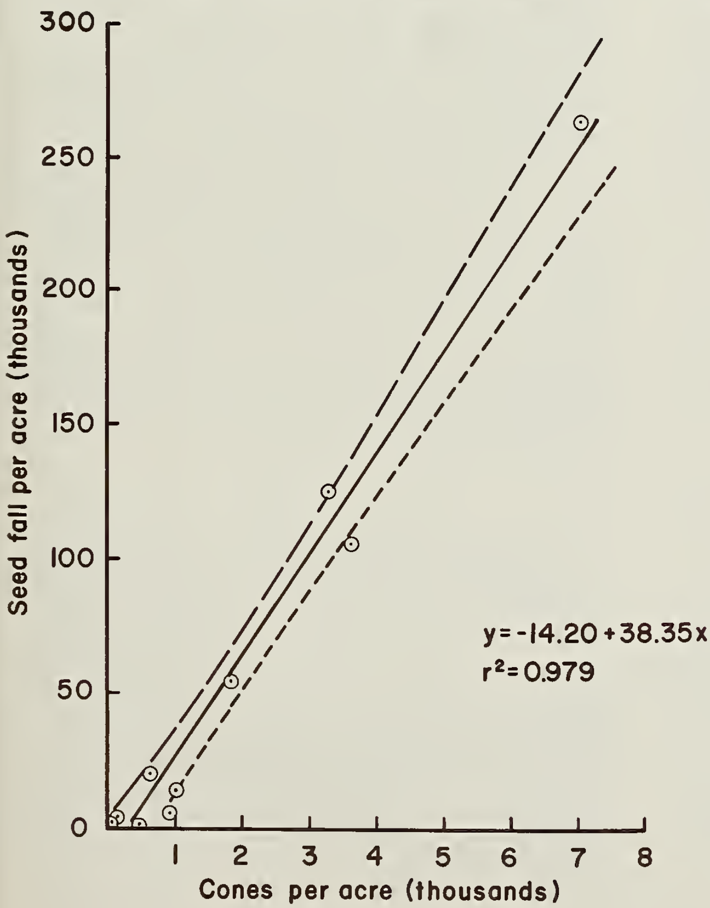

Figure 9.--Relationship of seed fall per acre (estimated from seed found in seedtraps) to production of undamaged cones per acre.

Seed Dissemination

Seed fall.—Seed fall per acre ranged from 263,360 in 1960 to only 1,040 in 1959 (table 4). Seed fall exceeded 100,000 seeds per acre when production of undamaged cones exceeded 3,000 per acre. A good linear relationship was found between the yearly seed fall and the number of undamaged cones produced ($Y = -14.20 + 38.35x$ with an $r^2 = 0.979$) (fig. 9). The relation between seed fall sample and the cone estimate in California was curvilinear when the number of cones was estimated on standing trees (Fowells and Schubert 1956).

The annual seed fall per acre was also related to the percent of conelet-bearing twigs ($r = 0.801$). The regression equation is $Y = -33.732 + 18.736x$, but since the standard error of estimate ($S\ y{\cdot}x$) is high (53,776), it should not be used to predict seed fall.

No information was obtained on seed flight and distribution. We know, however, that ponderosa pine trees do not effectively disseminate seeds over extensive areas (Fowells and Schubert 1956). Siggins (1933) measured the rate of fall of various lots of seed of several species in still air. From these rates of fall and an assumed tree height, the flight of seeds for various wind velocities can be calculated. For example, ponderosa pine seeds fall 15.2 feet per second in still air. Seed, falling 100 feet with a uniform wind of 10 miles per hour, would travel, on the average, about 294 feet horizontally. Barrett (1966) has recommended that ponderosa pine clearcuts should not exceed 5 chains in width.

The study area was well stocked with trees, but few, if any, seedlings became established during the 10-year study. The heavy seed fall of 1960 resulted in a literal carpet of new seedlings the following summer, but nearly all died during the ensuing winter and spring drought.

Seed quality.—The largest cone crops produced the best quality seeds. The large crops in 1960 and 1965 produced seeds that were at least 65 percent filled, compared to 10 to 45 percent for the smaller crops (table 4). For the 1965 crop, 72 percent of the seeds that fell before December 6 were filled, compared to only 54 percent for seeds that fell after that date. The average weight of filled early- and late-fallen seeds was the same (37 mg.), and germinated similarly (63 and 64 percent, respectively). In 1956, 91 percent of filled seeds germinated when planted in a greenhouse.

In California, the percentage of filled ponderosa pine seeds was also highest (72 to 79 percent) during years of heavy cone crops (Fowells and Schubert 1956). Other researchers have also noted that the first-fallen seeds are the most viable in this species (Squillace and Adams 1950, Curtis and Foiles 1961, Fowells and Schubert 1956). Curtis (1955) noted that ponderosa pine seeds from trees 60 to 160 years old in the northern Rocky Mountains were more viable than seeds from younger or older trees. Pearson (1923) found no differences in seed viability for trees 16 to 34 inches in diameter.

Time of seed fall.—Seeds in the seed traps were counted frequently as the 1965 crop fell, except when the traps were under snow. By October 26, only 0.5 percent of the current seed crop had fallen. By December 6, 64 percent had fallen, and by April 1, 1966, 95 percent of the total crop had fallen. Hence, nearly all seeds were shed in time to germinate the following summer. However, 26 percent of the 1960 seed crop fell between July 1 and September 26, 1961. No reason for this late seed fall is known, but similar occurrences may explain the occasional "delayed" germination of seed crops reported by Pearson (1950). More observations are needed to determine variations in the time of seed fall in the Southwest.

In California, Fowells and Schubert (1956) noted that strong, dry winds hastened seed fall, and that the majority of ponderosa pine seeds usually fell during October and November. In 1 year, however, these authors observed that 33 percent of the seed crop fell between November and August. In Idaho, seed fall from a heavy cone crop was 52 percent complete by September 15, and 90 percent complete by October 22 (Curtis and Foiles 1961).

Number of seeds per cone.—Cones averaged 31 seeds each, and the number of seeds per cone increased with the size of the cone crop. The five smallest cone crops, each less than 1,000 cones per acre, averaged only 14 seeds per cone compared to 33 for the five crops that exceeded 1,000 cones per acre. This is considerably less than the 70 seeds per cone reported for ponderosa pine in California (Fowells and Schubert 1956) and 64 to 92 seeds per cone for this species in Idaho (Curtis and Lynch 1957).

Silvicultural Considerations and Conclusions

Healthy, mature trees with exposed crowns and of large diameter are usually the best seed producers. Past fruitfulness, as indicated by the accumulation of old cones under a tree, is a good criterion for choosing seed trees (Downs 1947, Fowells and Schubert 1956, Pearson 1950). Also, cone production is a highly heritable trait (Matthews 1963). Therefore, the best trees to retain for seed production are those which:

1. Are about 24 to 28 inches in diameter.
2. Are dominant or free to grow.
3. Have a vigor class rating of A or B.
4. Are free of disease or heavy squirrel damage.
5. Show evidence of having produced good cone crops.
6. Have straight boles.
7. Have medium to small branches.

The number of seed trees needed to insure an adequate seed supply for regeneration cannot be stated with certainty. The periodicity of cone production was amply demonstrated during the present study. Large yearly variation in cone losses to squirrels and insects, and the consumption of seed on the ground by rodents and birds, make it almost impossible to determine what an "adequate" seed supply is. After seeds germinate, drought and frost heaving can wipe out the entire seedling crop (Larson 1960, 1961).

In the Southwest, Pearson (1950) somewhat arbitrarily recommended that six seed trees 18 inches d.b.h. or larger be left per acre after harvest. Results of the present study indicate that, if these trees are chosen with care, they could average 200 cones per year over a 5-year period. The total seed fall would be about 144,000 seeds, and of these, an estimated 72,000 (50 percent) would be sound. Pearson (1950) concluded that one seed in 100 survives to produce a seedling on moderately favorable sites. Thus, a final stocking of 720 trees per acre would result. It must be emphasized, however, that reliable guidelines must await the results of several harvest cuts.

Presently, planting seedlings on prepared sites is a much more certain way to establish new stands in the area adjacent to the Fort Valley Experimental Forest (Heidmann 1963). Another advantage of planting is that new stands may be genetically superior to those obtained from natural regeneration, if seed sources of planting stock are properly selected.

Abert squirrels are extremely destructive to cone crops. These squirrels destroyed more than 20 percent of the total 10-year cone production. Also, we observed that only the largest and best cones were taken by squirrels. Their twig-clipping activities are less destructive, and the loss of conelets was not considered serious. The squirrel population during the study was rated low, however; high squirrel populations may well preclude an adequate seed supply for natural regeneration in all but "bumper" crop years.

Cone losses to insects were not serious during the study.

The size of cone crops was closely related to the number of conelet-bearing twigs clipped by squirrels the previous winter and spring seasons. Therefore, the relative size of crops can probably be predicted on any area where squirrels clip twigs. Conelets abort mostly during the first growing season rather than during the following dormant season (Roeser 1941). Thus, the size of the conelet crop in October may accurately reflect the size of the cone crop a year later. Squirrels clip twigs after October, however, so the abundance of conelets must be determined from branch samples or by use of binoculars. Prediction of crops 1 year in advance, if reliable, would greatly aid in planning for seed-collection programs and site-preparation measures to obtain natural regeneration.

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1970. Cone crops of ponderosa pine in central Arizona, including the influence of Abert squirrels. USDA Forest Serv. Res. Pap. RM-58, 15 p., illus. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado 80521.

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Key words: *Pinus ponderosa*, conelets, cones, Abert squirrel

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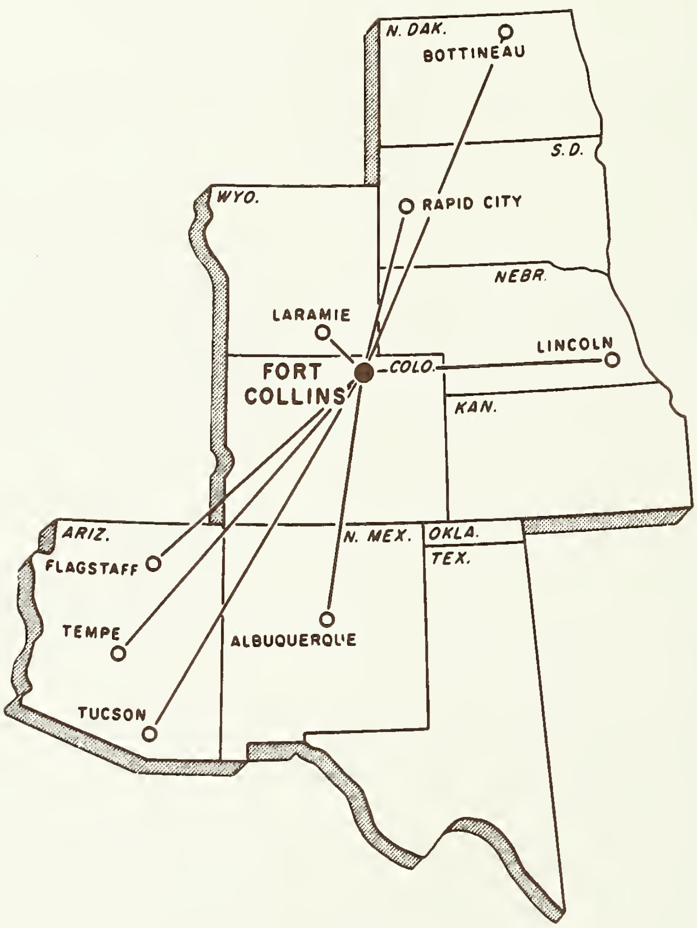
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